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PIT CONSTRUCTION BY ANTLION LARVAE: INFLUENCES OF SOIL ILLUMINATION AND SOIL TEMPERATURE

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Abstract.—Pits constructed by antlion larvae are most frequently found in areas which are darker and cooler than areas exposed to the sun. Soil illumination and soil temperature, therefore, are two factors which may play a role in determining the probability of pit construction. The influence of these factors upon the probability of pit construction by *M. immaculatus* larvae was examined. Soil illumination and soil temperature were independently varied in the laboratory. Soil temperature was found to have a significant effect upon pit construction, whereas soil illumination was found to have no such significant effect. This supports the view that the construction of pits in shaded areas is a response to temperature rather than to light.

Antlions of the genus *Myrmeleon* are best known for the ability of their larvae to construct inverted conical pits in dry, loose, fine grained soil. These pits provide the antlion larva with an effective means of capturing prey (Topoff 1977; Turner 1915). It has been frequently observed that antlion larvae begin constructing pits at, or immediately following sundown (Haub 1942; Topoff 1977; Wheeler 1930; Youthed and Moran 1969b). It has also been observed that antlion pits are usually found in shaded areas such as under ledges of rock, under logs which do not touch the ground at all points or under man made sources of shade (Green 1955; Haub 1942; Topoff 1977; Turner 1915). Shaded areas differ from areas exposed to the sun in two obvious respects; they are darker and they are cooler. These two characteristics also apply to any given area at or after sundown, when it is compared to the same area during the day. It therefore appears that soil illumination and soil temperature are two physical properties of the environment which may play a role in determining the probability of pit construction by antlion larvae.

In a series of laboratory experiments using larvae of *Myrmeleon immaculatus* (De Geer), Haub (1942) demonstrated that soil temperature does indeed influence the probability of pit construction. A similar result was demonstrated by Youthed and Moran (1969a) for larvae of *M. obscurus*

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(Rambur). Haub (1942) concluded that, "the building of pits after sundown is due to a temperature factor rather than light" (p. 116). However, he did not provide evidence to warrant the exclusion of light as a factor controlling the probability of pit building.

Antlion larvae appear to be well equipped to respond to light. Wheeler (1930) noted that the larvae possess seven eyes on each side of the head which appear to be transitional between ocelli and compound eyes. These eyes point in all directions except backwards. Behavioral responsiveness of antlion larvae to light has been reported. For example, Turner (1915) has demonstrated negative phototaxis in *M. immaculatus* and Comes (1909) found a similar result for *M. formicarius*.

Given the ability of antlion larvae to respond to light, the experiment discussed below attempts to determine whether the level of soil illumination influences the probability of pit construction by *M. immaculatus* larvae. In short, the study tests the validity of Haub's (1942) contention regarding the lack of control of light over pit construction. The study also attempts to replicate the findings of Haub (1942) and Youthed and Moran (1969b) regarding the influence of soil temperature upon probability of pit construction.

Materials and Methods

Forty-seven *M. immaculatus* larvae were used. All larvae were collected from the bank of a creek near the Southwestern Research Station of the American Museum of Natural History in southeastern Arizona. Only larvae found at the bottom of pits were used in the study. This insured that all antlion larvae used were capable of building pits under normal field conditions.

The experiment proper was carried out in an International Radiant Co. humidity chamber (Model H15) in which temperature and relative humidity could be independently regulated and thermostatically controlled. The chamber window was covered with cardboard to prevent ambient light from entering. Within the chamber, larvae were placed in one of two white plastic containers filled with 6 cm of dry silt. Each container was divided into two 11×16 cm compartments by a piece of cardboard and only one larva was placed in a compartment. Therefore, 4 larvae could be tested in each experimental session. A 75 W light bulb was used to illuminate the chamber in the high illuminance condition of the experiment and a 15 W bulb covered by a red translucent piece of plastic was used in the low illuminance condition. A Gossin Lumasix light meter was used to measure the illuminance at the silt surfaces within the chamber. Petri dishes containing 0.5 cm of dry silt were used to store the larvae between the time of collection and the time of testing.

The 4 larvae and the silt in which they were to be tested were collected 3 h prior to each session. This was the approximate amount of time needed for the silt to reach its desired temperature after being placed in the environmental chamber. During this 3 h period, the larvae were stored in a shaded area of the laboratory. The experiment was run as a 2 × 2 factorial design with 2 temperature levels (hot and cool) and 2 illumination levels (light and dark). Therefore, 4 different experimental conditions were used: (1) hot-light, (2) hot-dark, (3) cool-light and (4) cool-dark. Each experimental condition was run 3 times, making a total of 12 test sessions, and each session lasted 3 h. All testing was done between 1200 and 2200 h (MST). Each time a condition was repeated, it was run at one of 3 different times during the day: early afternoon, late afternoon or evening. These periods often overlapped by as much as 1 h. A total of 12 larvae were tested under each experimental condition, except that due to the death of one larva, only 11 were tested under the hot-light condition. The silt temperature was checked at the beginning and the end of each test session. Silt temperatures in the hot conditions ranged from 38–47°C whereas temperatures in the cool conditions ranged from 20–24°C. The measured silt surface illuminance was 1,076 lx in the light conditions and 86 lx in the dark conditions. At the beginning of each test session, one larva was placed on the surface of each silt compartment within the environmental chamber. Three hours later, each compartment was checked for pit construction. A larva was scored positive for pit construction if: (1) a pit existed in its compartment, or (2) the larva was in the process of pit construction and had dug out more than one concentric circle. Larvae which were not scored positive for pit construction were placed in a box of silt and checked for pit construction 24 h later. All these larvae built pits and this ruled out physical damage during the experiment as a reason for lack of pit construction.

Results

The mean percentage of larvae constructing pits, per session, was determined for each condition of the experiment. The greatest amount of pit construction occurred in the cool-dark condition (58.3%), followed in descending order by the cool-light condition (41.7%), the hot-light condition (11.0%) and the hot-dark condition (8.3%). The mean percentage of larvae constructing pits was 9.7% per session under the hot temperature level as compared with 50.0% per session under the cool temperature level. Under the light illumination level, the mean percentage of larvae constructing pits was 26.3% per session as compared with 33.3% per session under the dark illumination level. A two-way ANOVA in conjunction with the arcsine transformation for percentage data revealed a significant difference between the two temperature levels ($F = 9.16$, df $= 1,8$, $P < 0.025$). No significant difference was found between the two illumination levels (F = 0.30, df = 1,8, $P > 0.05$) nor was any significant interaction found between temperature and illumination (F = 0.48, df = 1,8, $P > 0.05$).

The overlap of the early afternoon, late afternoon and evening replicates within each condition prevented the inclusion of time of day as a separate factor in the design. However, since the early afternoon and evening time periods never overlapped, differences in pit building activity during these two time periods were examined. The mean percentage of larvae constructing pits was 12.5% per session during the early afternoon time period (1230 to 1530 h) and 39.5% per session during the evening time period (1835 to 2200 h). A single classification ANOVA in conjunction with the arcsine transformation for percentage data revealed a significant difference between the two time periods (F = 6.34, df = 1,6, $P < 0.05$).

Discussion

The finding that the greatest amount of pit building took place under the cool-dark condition is consistent with field observations that antlion larvae frequently build pits in areas that are darker and cooler than nearby areas exposed to the sun (Green 1955; Haub 1942; Turner 1915). The significant difference in pit building behavior between the two temperature levels (hot and cool) supports the finding of Haub (1942) that soil temperature can influence the probability of pit construction in *M. immaculatus* larvae. It is interesting to note that Haub found no pit construction above 28°C and 100% mortality above 38°C. This did not appear to be the case in the present study since pit construction occurred at temperatures as high as 44°C and only one out of 24 larvae died within a temperature range of 38–47°C. It seems that larvae in the present study were better able to withstand and function at high temperatures than the larvae used by Haub. Although both studies employ *M. immaculatus* larvae, those used in the present study were collected in Arizona whereas those used by Haub were collected in Ohio. A comparison of summer soil temperatures measured in the field suggests that this seemingly greater tolerance for high temperatures by Arizona *M. immaculatus* larvae may represent a regional adaptation to higher temperature extremes than those encountered by Ohio *M. immaculatus* larvae.

The absence of a significant difference in pit building behavior between the two illumination levels (light and dark) supports the view that the construction of pits after sundown or in shaded areas is a response to temperature rather than to light. In other words, frequent construction of pits in cool, dark areas is probably a response to coolness as opposed to darkness. The absence of an influence of illumination level upon pit building probability was most likely not due to an inability of the larvae to discriminate between the illumination levels used since Youthed and Moran (1969b) found that antlion larvae (*M. obscurus*) can discriminate between illumination levels similar to those used in the present study.

The significant difference in pit building activity found between the early afternoon and evening time periods seems to indicate endogenous temporal variation in pit building since external conditions were the same during both periods. This would be in agreement with findings of Youthed and Moran (1969b) who demonstrated an endogenous circadian pit building rhythm in *M. obscurus* larvae. Pit building in *M. immaculatus* larvae therefore appears to be under the control of internal as well as external factors.

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